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Genetics, Geography, and Culture: The Population of S. Pietro Island (Sardinia, Italy)

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ABSTRACT An interesting aspect of the island of Sardinia (Italy) is the wide range of genetic variability within the island itself. The variability is widened by the presence of some populations of different ethnic origin who speak a language other than Sardinian.

This work deals with the study of the genetic structure of the Carloforte population which inhabits the tiny island of S. Pietro 4 km off the southwest coast of Sardinia. S. Pietro was first populated in 1738 by emigrants coming from the island of Tabarka (Tunisia) who spoke an archaic form of the Ligurian dialect.

Data on genetic polymorphisms in the Carloforte population are presented and discussed in relation to some Sardinian and Italian populations. Data on demographic and matrimonial structure are also presented.

The genetic analyses show the Carloforte population as being clearly separated from both Sardinians and continental Italians.

The isolation of Carloforte, highlighted by language diversity, endogamy, and consanguinity levels and marriage area, supports the idea of genetic diversity linked to cultural peculiarity.

In the western Mediterranean area, the population of the island of Sardinia (Italy) provides a well documented example of a genetic isolate among European populations. Its origin probably goes back to the middle Pleistocene, with rather limited influences from different Mediterranean groups during pre- and historical times.

An important feature of Sardinia is the high genetic heterogeneity within the island itself due to geographical and/or cultural fragmentation into numerous isolates (Moroni et al., 1972; Workman et al., 1975; Floris and Vona, 1980, 1984; Piazza et al., 1985; Modiano et al., 1986; Griffo et al., 1988; Ulizzi et al., 1988; Floris-Masala et al., 1989; Gatti, 1990; Marini, 1990; Succa et al., 1990; Gruppioni et al., 1991; Walter et al., 1991; Contu et al., 1992; Vona et al., 1992; Morelli, 1993; Brasili Gualandi et al., 1994; Moral et al., 1994).

This work deals with the study of the genetic structure of a Sardinian linguistic isolate: the population of Carloforte (Fig. 1). Nowadays the people of Carloforte speak an archaic form of the Pegli dialect. Pegli was once a small village in Liguria (Italy) which has now been swallowed up by the urban fabric of Genova (Fig. 1). The town of Carloforte is on the tiny island of S. Pietro about

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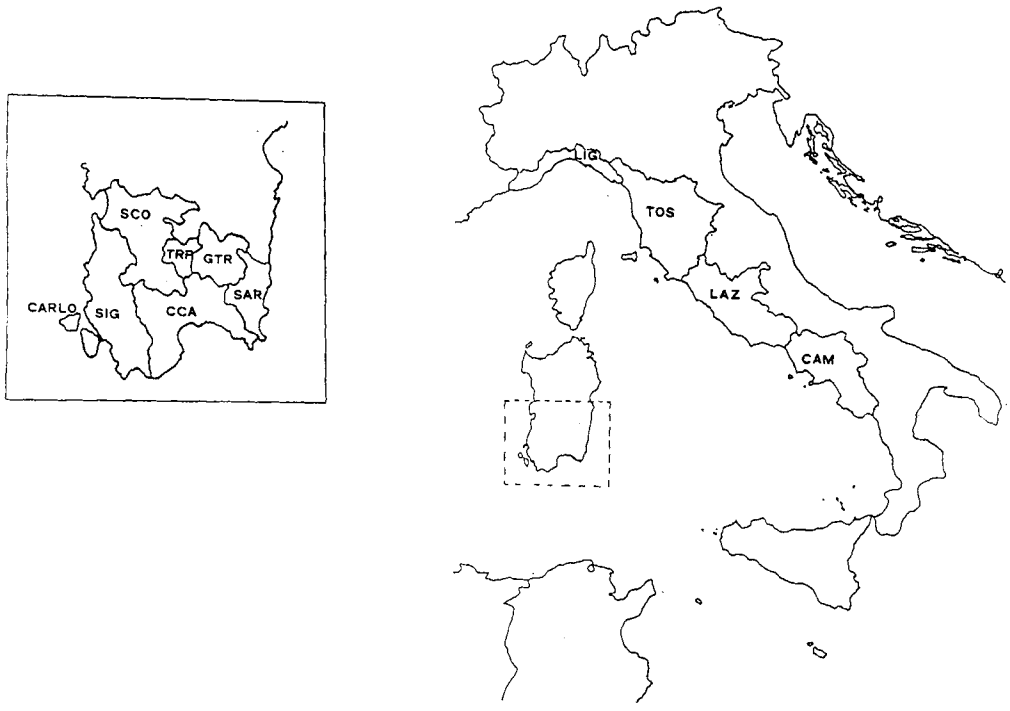

Fig. 1. Geographic position of Carloforte (Sardinia, Italy) and of the comparison populations (CARLO = Carloforte; SIG, Sulcis-Iglesiente; CCA, Campidano Cagliari; SAR, Sarrabus; TRP, Trexenta-Parteolla; GTR, Gerrei-Trexenta; SCO, South Campidano Oristano; CAM, Campania; LAZ, Lazio; TOS, Toscanna; LIG, Liguria; T, Tabarka).

4 km off the southwest coast of Sardinia. It lies on latitude 39°8′ north and longitude 8°13′30″, east and covers an area of 5 km^2.

Historical evidence shows that S. Pietro island was first populated in 1738, the year that Carloforte was founded. Before that it had occasionally been a refuge for shipwrecked sailors and pirates but had no permanent settlements. In 1738 the king of Sardinia, Carlo Emanuele III of Savoy, allowed a group of inhabitants from Tabarka, an island lying between Bona and Biserta in Tunisia, to colonize the island of S. Pietro. The inhabitants of Tabarka were the descendants of families which had emigrated from Pegli in 1542, when emperor Carlo V gave them coral fishing rights on the same island. The community of Tabarka had very little contact with the north African populations, although they kept up relations with their origins. At the beginning of the 18th century a long period of economic prosperity came to an end with the impoverishment of the coral banks. Since relations with the Bey of Tunis and Algiers had also greatly deteriorated, the Tabarkini left their island and migrated to Sardinia, settling on the island of S. Pietro.

Taking advantage of the relatively recent and therefore demographically complete history of the population of Carloforte (about 10 generations), a genetic analysis based on 12 classic systems was performed. The results are discussed in relation to demographic information without needing to make assumptions, as is usual in the interpretation of studies of this kind.

MATERIAL AND METHODS

Demographic structure

We collected data on the matrimonial structure and demographic changes of the population of Carloforte. We analyzed en-

dogamy, marital distances, and consanguinity from the founding of Carloforte in 1738 to the year 1993, drawing on data from parish registers kept at the Bishop's see at Iglesias and the parish of Carloforte. Except for the first and last periods, the data were grouped into 25 year periods. Marital exogamy was defined as the frequency of individuals born outside Carloforte, but who married there. Marital distances were calculated as the crow flies between Carloforte and the birth place of spouses. The average consanguinity rate was calculated by the Bernstein coefficient (alpha) (1930).

Genetic analysis

The genetic systems of a sample of 141 unrelated, apparently healthy individuals of both sexes, born and residing in Carloforte, with native-born parents and grandparents, were analyzed. Blood samples were collected in sterile test tubes containing the anticoagulant EDTA at the Civil Hospital in Carbonia and transported to the Laboratory of Anthropological Sciences Section at Cagliari University. Here the serum was separated from the erythrocytes, which were then washed three times in a saline solution. Both the sera and the hemolysates were divided into parts, some of which were transferred to the Laboratory of Anthropology at Barcelona University (Spain). In the two laboratories 12 classic markers for a total of 34 alleles and haplotypes were determined overall. The frequencies of the following markers were examined: the blood systems AB0, RH, and MN were studied by the standard methods. 6-phosphogluconate dehydrogenase (PGD), adenylate kinase (AK), phosphoglucomutase (PGM1), and NADH diaphorase (DIA) phenotypes were analyzed using the methods of Harris and Hopkinson (1976) with slight modifications. Acid phosphatase (ACP1) and esterase D (ESD) types were determined by the Grunbaum method (1981). The method of Bissbort et al. (1978) was used to obtain the subtypes of PGM1. The phenotypes of haptoglobin (HP) and group-specific component (GC) were determined by isoelectrofocusing on polyacrylamide gels (PAGIF) using standard laboratory procedures. Sialidase pretreatment of samples was performed for PLG and F13A. TF and PI subtypes were determined by protein fixation and staining with Coomassie blue. Immunoprinting for GC and gel immunofixation for PLG and F13A were carried out with monospecific antisera. ORM, PLG, and F13A bands were detected by silver staining according to Montiel et al. (1988), with some modifications. C3 types were determined by the Germenis and Babionitakis method (1982).

RESULTS

Demographic structure

Population growth. In 1738 Carloforte's founding nucleus numbered 86. In the same year other Tabarkini and families from Pegli joined this nucleus, bringing the number of inhabitants to 469. Over the following decades the population increased steadily until 1798 when the town was destroyed by the Rais of Tunis. After the reconstruction of the town the population grew steadily, reaching maximum development at the beginning of the 1930s. From then on there was a decrease which brought the 8,100 strong population of 1931 to 6,630 in 1991 (Casalis, 1836; Ferraro, 1989; Luxoro, 1977; Vallebona, 1974, 1975; I.S.T.A.T., 1993).

Matrimonial structure. From 1738 to 1993 75.42% of the marriages which took place in Carloforte were endogamous. The highest frequency of endogamy (91.76%) appears between 1825 and 1849, and the minimum value (50.45%) was calculated between 1975 and 1993. A similar value (55.56%) was found in the initial 1738–1749 period, due to the arrival of many individuals coming mainly from Pegli.

The overall average marriage distance, based on the total number of marriages, was 42.36 km, with higher values for men than for women. The greatest marriage distance occurs in the first period (1738–1749) and is almost always at least three times greater than the distances of the later periods.

Most (65.6%) of the exogamous marriage partners over the total time period are from Sardinia. The remaining are mainly from continental Italy, and particularly from Liguria, Campania, Lazio, and Toscana.

The influence of exogamous marriages on the genetic structure of the Carloforte popu-

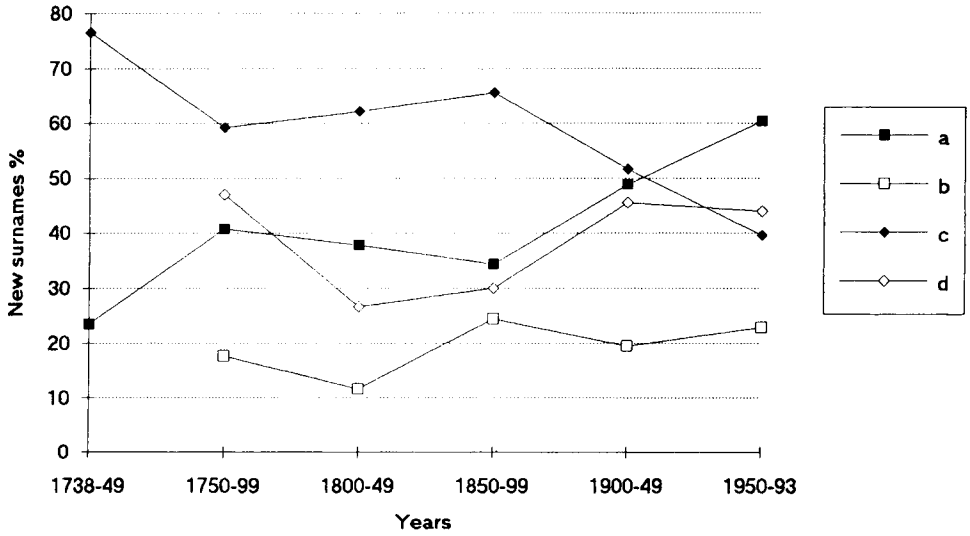

Fig. 2. Frequencies of surnames which appear in Carloforte for the first time in each period and which disappear in later periods (a, new Sardinian surnames; b, lost Sardinian surnames; c, new Italian surnames; d, lost Italian surnames).

lation is much more limited than could be supposed from their frequency. A preliminary examination of surnames present in the Carloforte community during the various periods shows the gradual appearance of 682 new surnames, 59.68% of which disappear at later dates. In all the periods most of the new surnames come from regions of continental Italy, and only in the last period do new surnames of Sardinian origin become more frequent (Fig. 2).

The Sardinian contribution was furthermore expressed in the relations between the number of spouses of Sardinian origin and the total number of individuals married in Carloforte. To evaluate this and the contribution of the other regions the same procedure was followed. We added twice the number of exogamous marriages between Sardinians (2×) to the number of marriages between one Carlofortine and one Sardinian (Y). The sum was then divided by double the number of marriages (2× + Y)/2N. Figure 3 shows that, from the founding of Carloforte until the end of the last century, the spouses of the exogamous marriages came mainly from continental Italy. From the beginning of this century the trend has turned about and Sardinians are more often preferred in matrimonial choices. Of the total number of marriages which took place between 1738 and 1993, 6.73% were between blood relatives, with an alpha value equal to 1.63×10^{-3}. The 1775–1799 period has the highest consanguinity coefficient value with 29.57% of consanguineous marriages (alpha = 4.58×10^{-3}). Between 1975 and 1993 there were no marriages between blood relatives.

Genetic analysis

Allele frequencies. Table 1 shows the allele and haplotype frequencies of the 12 markers used in the genetic analyses. In general, the allele frequencies found in the population of Carloforte generally fall within the variation range of both Sardinian and continental Italian populations.

Compared to Sardinians the blood groups of the Carloforte population show a higher frequency for the haplotype RH*cde and a lower frequency for the allele MN*M and the haplotype RH*Cde. Compared to other Italians, our population shows higher frequencies for AB0*Ø, MN*M, and RH*Cde and lower ones for the RH*cde haplotype and ACP*A, PGM1*1F, and ESD*1 alleles. The frequency of the allele ESD*1 is also lower than that of the Sardinians. The frequencies of the alleles PGM1*2S and HP*1 of Carloforte are above the topmost limit of

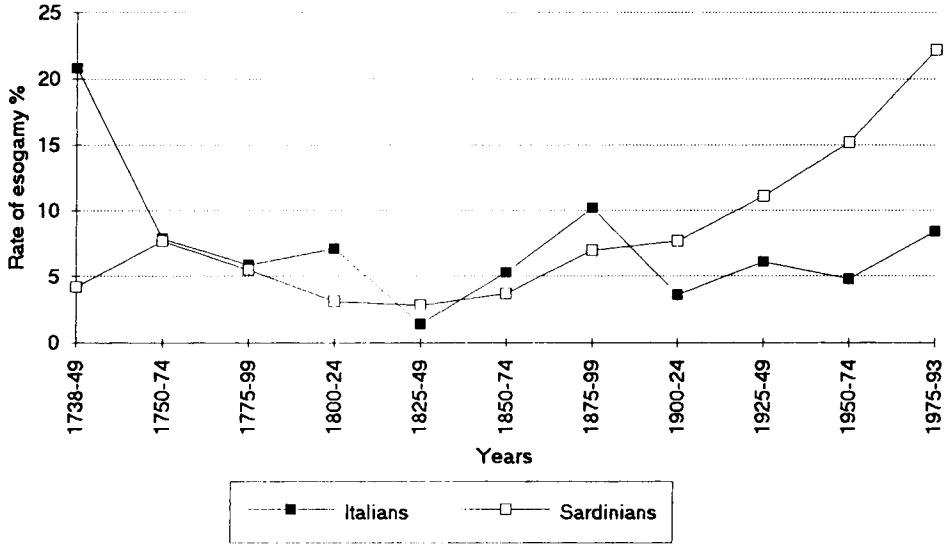

Fig. 3. Origin of exogamous marriage partners in the Carloforte population.

the frequency range reported for Sardinians and other Italians. For the allele GC*1S, on the other hand, the sample from the island of S. Pietro is below the lowest limit of the variability field.

The values of G^2 heterogeneity (Sokal and Rohlf, 1969) shown in Table 2 were calculated by comparing Carloforte with each of the Table 1 populations. Comparisons between Carlofortini and other Sardinians for the RH, ESD, and GC systems are particularly significant, whereas the ACP, ESD, and HP systems appear mainly heterogeneous.

Genetic distances. To have an overall evaluation of the genetic relations existing between Carloforte and the other populations we used Reynolds' (1983) genetic distances. The least distance obtained was between two continental regions (TOS-LAZ), whereas the greatest distance occurs between Liguria (LIG) and the Sardinian region of Trexenta-Parteolla (TRP). The distances obtained by comparing the Carloforte population with Sardinian populations vary from 15.3×10^{-3} (GTR) to 27.5×10^{-3} (TRP), while the range for the comparison with the continental regions varies from 8.5×10^{-3} (LAZ) to 17.8×10^{-3} (LIG). Many of the distances between Carlofortini and Sardinians are greater than those between Carlofortini and continental Italians. The distances between Sardinian populations vary between 2.6×10^{-3} (GRT-SCO) and 12.4×10^{-3} (SAR-TRP); those between continental Italian populations have a lower range: from 0.7×10^{-3} (LAZ-TOS) to 8.0×10^{-3} (LIG-CAM). Greater values of the distances were calculated between Sardinians and continental Italians: from 18.5×10^{-3} (CCA-LAZ; SAR-LAZ) to 43.6×10^{-3} (TRP-LIG).

Apart from the marked difference between Sardinians and other Italians, the results highlight greater variability within the Sardinian populations and lower variability within Italian populations. The particular genetic position of Carloforte midway between Sardinians and continental Italians, while tending to be genetically closer to the Italians, is evident (Fig. 4).

A graphic picture of the genetic distances was carried out by the neighbor-joining tree method of Saitou and Nei (1987) (Fig. 5). The tree shows that the greatest degree of divergence is between the Sardinians and continental Italians, and that although the population of Carloforte lies midway between the two extreme groups it is slightly closer to the continental populations, thus confirming what had previously been observed.

TABLE 1. Gene frequencies of the Carloforte and comparison populations

		Sardinian[1]							Mainland Italian[1,2]			
		CARLO[2]	SIG	CCA	SAR	TRP	GTR	SCO	CAM	LAZ	TOS	LIG
ABO	A	0.229	0.261	0.240	0.218	0.224	0.203	0.203	0.216	0.237	0.247	0.254
	B	0.040	0.073	0.068	0.061	0.058	0.059	0.067	0.088	0.079	0.072	0.075
	0	0.731	0.666	0.692	0.721	0.718	0.738	0.730	0.696	0.684	0.681	0.671
RH	CDE	0.015	0.016	0.007	0.004	0.011	0.008	0.007	0.009	0.008	0.007	0.003
	CDe	0.514	0.698	0.683	0.696	0.689	0.709	0.704	0.517	0.485	0.465	0.420
	cDE	0.102	0.114	0.107	0.111	0.113	0.083	0.102	0.134	0.121	0.119	0.111
	cDe	0.083	0.067	0.043	0.029	0.187	0.023	0.066	0.041	0.025	0.022	0.018
	Cde	0.000	0.001	0.001	0.001	0.000	0.003	0.000	0.020	0.014	0.019	0.010
	cdE	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.005	0.004
	cde	0.285	0.104	0.158	0.159	0.000	0.174	0.121	0.277	0.346	0.363	0.434
MN	M	0.589	0.676	0.676	0.651	0.685	0.671	0.697	0.538	0.563	0.537	0.588
	N	0.411	0.324	0.324	0.349	0.315	0.329	0.303	0.462	0.437	0.463	0.412
ACP	A	0.144	0.206	0.266	0.125	0.186	0.193	0.106	0.293	0.262	0.271	0.280
	B	0.781	0.713	0.643	0.797	0.701	0.719	0.802	0.667	0.681	0.665	0.668
	C	0.075	0.081	0.091	0.078	0.113	0.089	0.092	0.040	0.057	0.064	0.052
ESD	1	0.797	0.856	0.884	0.908	0.914	0.847	0.884	0.866	0.853	0.857	0.862
	2	0.203	0.144	0.116	0.092	0.086	0.153	0.116	0.134	0.147	0.143	0.138
	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000
PGM1	1S	0.640	0.640	0.689	0.684	0.655	0.671	0.684	0.578	0.598	0.601	0.602
	1F	0.079	0.103	0.092	0.084	0.085	0.080	0.094	0.127	0.123	0.110	0.107
	2S	0.243	0.215	0.192	0.207	0.233	0.215	0.173	0.240	0.230	0.235	0.226
	2F	0.037	0.042	0.027	0.025	0.027	0.034	0.049	0.055	0.049	0.054	0.065
AK	1	0.993	0.966	0.980	1.000	0.946	0.991	0.987	0.971	0.940	0.967	0.958
	2	0.007	0.034	0.020	0.000	0.054	0.009	0.013	0.029	0.036	0.033	0.042
6PGD	A	0.982	0.967	0.975	0.991	0.994	0.972	0.968	0.974	0.994	0.966	0.979
	C	0.018	0.033	0.025	0.009	0.006	0.028	0.032	0.026	0.006	0.034	0.021
DIA	1	0.996	1.000	0.996	0.996	1.000	0.996	0.994	0.994	0.997	0.994	0.994
	2	0.004	0.000	0.004	0.004	0.000	0.004	0.006	0.006	0.003	0.006	0.006
GC	1S	0.536	0.674	0.680	0.724	0.696	0.700	0.739	0.549	0.580	0.606	0.673
	1F	0.145	0.022	0.054	0.112	0.065	0.053	0.009	0.165	0.143	0.139	0.107
	2	0.319	0.304	0.266	0.164	0.239	0.247	0.252	0.286	0.277	0.255	0.220
	V	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.001	0.000
C3	S	0.814	0.771	0.817	0.787	0.809	0.805	0.825	0.808	0.808	0.805	0.812
	F	0.175	0.229	0.183	0.213	0.191	0.195	0.175	0.188	0.188	0.193	0.181
	V	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.004	0.002	0.007
HP	1	0.436	0.390	0.376	0.415	0.379	0.348	0.385	0.323	0.355	0.351	0.300
	2	0.564	0.610	0.624	0.585	0.621	0.652	0.615	0.677	0.645	0.649	0.700

[1] Vona, unpublished data.
[2] Beretta et al., 1985; Biondi et al., 1989; Dominici et al., 1986; Lucarelli et al., 1973; Piazza et al., 1989; Roychoudhury and Nei, 1988; Scacchi et al., 1987; Seefried-Lehmann et al., 1992.
[3] CARLO, Carloforte; SIG, Sulcis-Iglesiente; CCA, Campidano Cagliari; SAR, Sarrabus; TRP, Trexenta-Parteolla; GTR, Gerrei-Trexenta; SCO, South Campidano Oristano; CAM, Campania; LAZ, Lazio; TOS, Toscanna; LIG, Liguria.

TABLE 2. Values of G^2 heterogeneity between Carloforte and each of the comparison populations

	ABO	RH	MN	ACP	ESD	PGM1ief	AK	6PGD	DIA	GC	C3	HP
SIG[2]	1.566	19.288**	3.246	4.809	4.807*	1.069	6.119*	1.519	1.598	14.881**	7.613	0.848
CCA	2.188	14.677**	3.046	21.012**	13.280**	9.619*	2.597	0.476	0.002	18.383**	6.431	3.425
SAR	1.397	14.720**	1.681	0.387	12.089**	7.330	2.367	0.692	0.008	14.868**	3.939	0.332
TRP	0.708	10.288*	1.507	4.056	15.862**	2.165	9.316**	1.440	1.262	14.024**	2.211	1.994
GTR	0.809	13.841**	1.992	2.442	2.617	2.441	0.044	0.616	0.004	14.449**	3.305	1.735
SCO	2.347	14.086**	3.531	3.402	14.048**	5.345	0.779	1.814	0.175	44.801**	8.826	1.304
CAM	3.659	47.366**	1.255	35.777**	9.329**	6.759	6.297*	0.832	0.299	1.116	1.937	10.624**
LAZ	3.670	6.081	0.334	20.447**	5.627*	5.452	8.853**	2.694	0.027	2.479	1.937	7.059**
TOS	2.768	7.546	1.264	20.676**	5.537*	4.149	5.225	1.927	0.179	5.959	4.792	8.647**
LIG	3.504	15.315**	0.000	25.406**	3.535	6.195	11.974**	0.027	0.184	13.613**	0.325	14.644**
df	2	4	1	2	1	3	1	1	1	2	2	1

[2] SIG, Sulcis-Iglesiente; CCA, Campidano Cagliari; SAR, Sarrabus; TRP, Trexenta-Parteolla; GRT, Gerrei-Trexenta; SCO, South Campidano Oristano; CAM, Campania; LAZ, Lazio; TOS, Toscanna; LIG, Liguria.
* $P < 0.05$.
** $P < 0.01$.

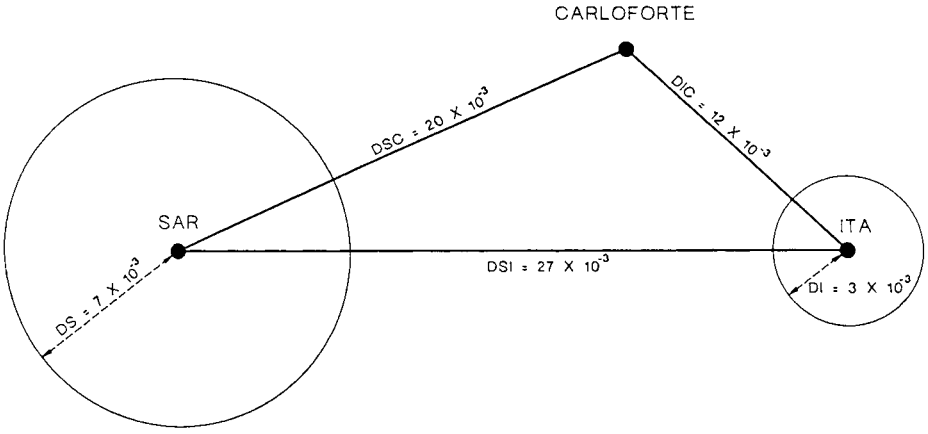

Fig. 4. Genetic relations between Carloforte, Sardinians (SAR), and continental Italians (ITA) taken from the averages of genetic distances. DS, distance within Sardinians; DI, distance within Italians; DSC, distance between Sardinians and Carloforte; DSI, distance between Sardinians and Italians; DIC, distance between Italians and Carloforte.

Principal components. The study of variability between the populations was also achieved by the analysis of the principal components. The first two components together account for 56.3% of the total variance, being 41.4% and 14.9%, respectively. Single gene contribution to the two components differs. Greater weight in the first component is attributed to the alleles RH*CDE, MN*M, ACP*A, PGM*1S, GC*1S, C3*V, and HP*1, which show a strong correlation ($r > 0.7$) with the first component. The alleles which have greater influence in the second component are ESD*1 and AK*1 ($r > 0.7$). In Figure 6, which shows the projection of the populations within the space defined by the first two components, the distance of Carloforte both from other Sardinian populations and continental Italians is evident. The first component clearly separates Carlofortini and Sardinians from the continental populations. The second component shows the particular position of the Carloforte population compared to other Sardinian populations.

Genetic admixture. The admixture level of the Carloforte population with Sardinians and continental Italians was evaluated using the method proposed by Chakraborty et al. (1992). The evaluation of admixture was based on the average genic frequencies taken from Table 1. Homogeneity of the values relative to each locus is shown by the nonsignificant value of the X^2 total ($X^2 = 0.624$; $df = 11$). The value of the admixture coefficient ($m = 0.621 \pm 0.341$) indicates that the population of continental Italy had a slightly higher influence on the Carloforte gene pool.

Similar values are reached calculating the m parameter by the Cavalli-Sforza formula (1994), starting from the genetic distances. The contribution by continental Italian populations to the Carloforte gene pool is 0.648; the Sardinian contribution, instead, is 0.352. Assuming that the proportion of Sardinian genes entering Carloforte has been constant through each generation, the estimate of the admixture rate per generation would be $m = 4.25\%$.

DISCUSSION

Data presented here show that the Carloforte population lived in fairly strict isolation, the level of which has decreased sharply only in recent decades.

The population of Carloforte shows some gene frequencies that distinguish it from Sardinians and from those continental Italian populations which, through the exogamous marriages, made a greater genic contribution to it. The resulting genetic characteristics would place the Carloforte population midway between Sardinians and

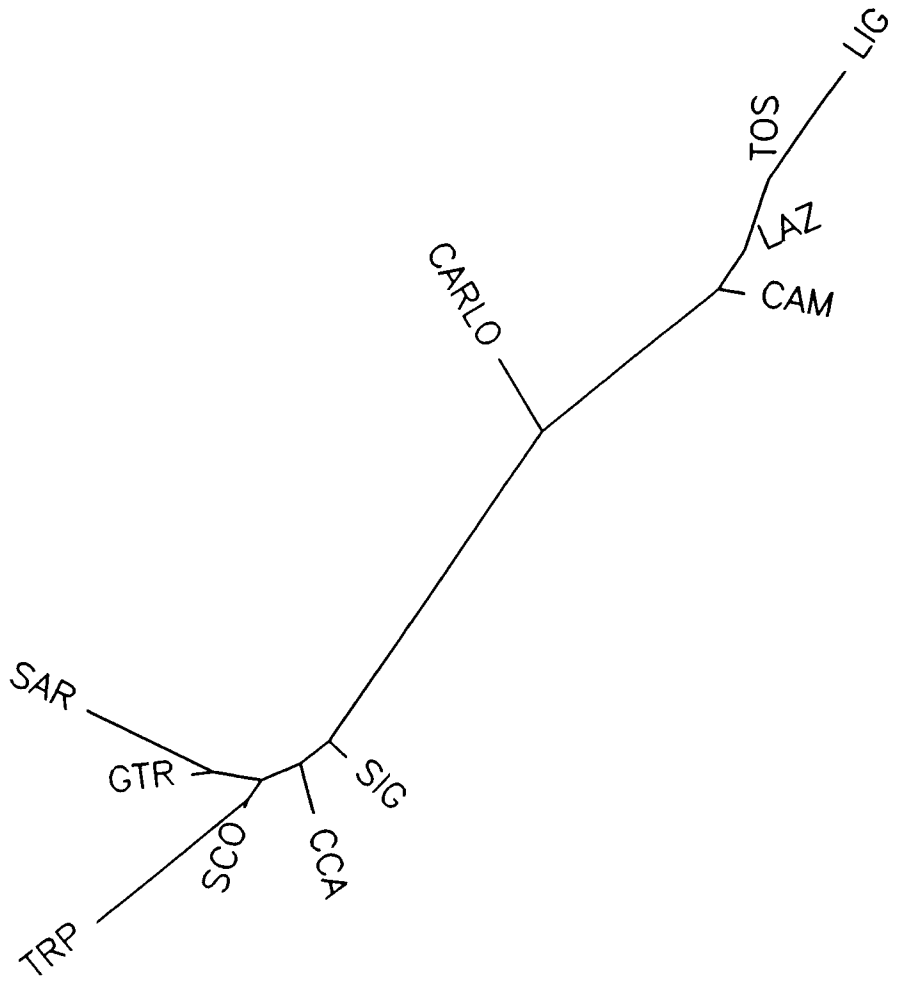

Fig. 5. Neighbor-joining tree taken from the matrix of the genetic distances. Abbreviations as in Figure 1.

other Italian populations. Taking into account the indications from the neighbor-joining tree, the admixture coefficient, and the average values of genetic distances, however, it can be reasonably argued that even today, albeit in modest degree, it is the continental rather than the Sardinian component which prevails.

However, greater genetic homogeneity could have been expected between the Carloforte population and the other Sardinian populations. This diversity from the Sardinians, which still exists, can be explained in different ways. Besides the different ethnic substratum of the two populations and a geographical closeness limited to a period of about 10 generations, other causes relating to the evolutionary characteristics of the Sardinians need to be considered: the division of the territory and populations into cantonal areas; the difficulty in communication networks between areas, which favored strict isolation; and low population density, which in some periods was considerably reduced by a bottleneck effect and genetic drift.

The genetic diversity between Carloforte,

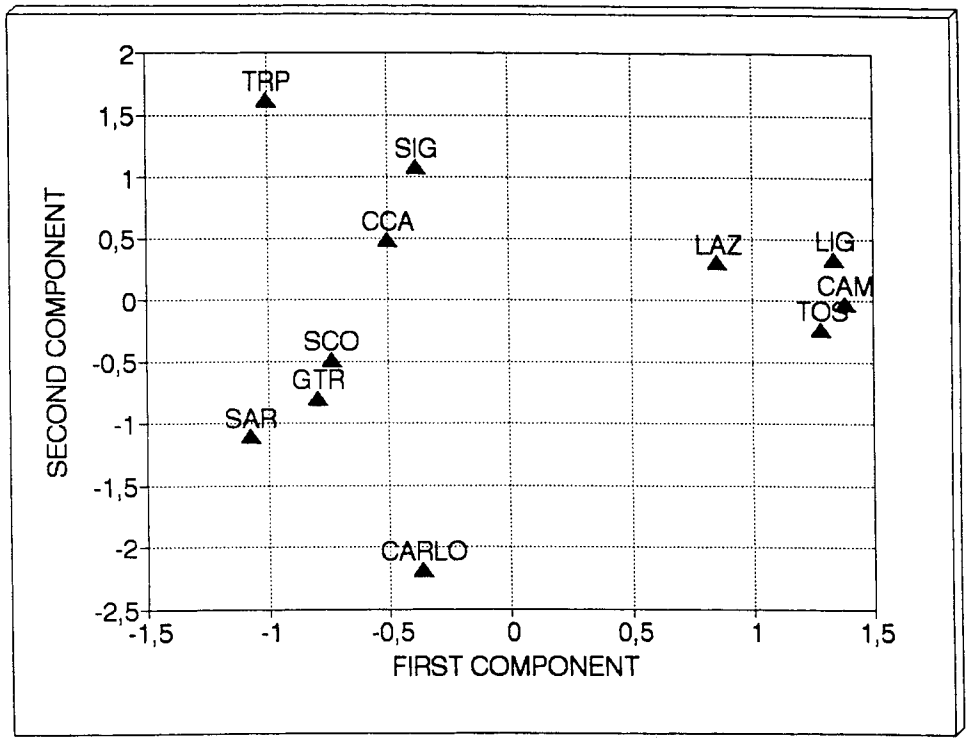

Fig. 6. Plot of the first two principal components. Abbreviations as in Figure 1.

Sardinia, and continental Italy is mainly to be ascribed, however, to the historical events through which the three groups lived. Sardinia and Carloforte, unlike other Italian regions, went through a long period of considerably strict geographic and cultural isolation. This helped to keep their cultural and genetic identity distinct even from the Italians of the Peninsula. The geographic and cultural isolation of Carloforte, highlighted by the diversity of language, high endogamy levels, limited marriage area, and considerable consanguineity, had a conservative effect on those characteristic genetic traits probably already present in the small founding nucleus.

In relation to the Sardinian genetic influence on Carloforte, analysis of the matrimonial structure indicates an early presence of the Sardinian component. On the basis of demographic information (Fig. 3), the infusion of genes did not lead to genetic assimilation of the Carloforte population into the surrounding gene pool because mainland Italians also provided a continuous genetic infusion into Carloforte.

The consistent breaking down of isolation, as shown by the recent marked increase of exogamous marriages, the disappearance of consanguineous marriages, and the fact that matrimonial choices are more and more inclined exclusively toward Sardinia, lead us to predict further genetic incorporation of the Carlofortini gene pool into that of the Sardinians.

Finally, the analysis of the genetic and matrimonial structure of the Carloforte population suggests that genetic diversity is linked to cultural diversity. The great difference in language spoken in Carloforte and in other Sardinian groups may have formed a partial barrier to genetic exchanges, a barrier which seems to be abating over time.

Despite the proximity of the island of S. Pietro to Sardinia, the genetics and language of Carloforte even today echo the genetic and linguistic characteristics of its founders. However, linguistic difference is not likely

to have been the sole cultural factor that served to restrict gene flow. A small island has limited economic resources. The economy of the island of S. Pietro is based on the sea. Its inhabitants were, and in part still are, mainly sailors and fishermen, who were more likely to find marital partners in their home town or off shore than on the lands around Carloforte. Only recently has the island's economy been boosted by the development of tourism.

In the last decade, some studies support a model of genetic differentiation based on geographical and cultural factors. The associations between geography, language, and genetics, however, are not always evident. In this case the Carloforte population shows how genetic and linguistic information together can, in contrast to geographical evidence alone, prove the origin of a specific population. The historic record provides the verification of the linguistic evidence, which points to a Ligurian dialect origin, and the genetic evidence that places the Carloforte population between the surrounding Sardinia and mainland Italy.

In conclusion, the results obtained on the concordance between demographic and genetic data lead us to believe that the study of a population's structure can, even in the absence of demographic data, be correctly and reliably carried out using only genetic markers. From the conclusions reached by various authors based on classic markers and DNA we maintain, moreover, that the biological history of a population can be well analyzed using the traditional and less expensive markers.

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LITERATURE CITED

Beretta M, and Santachiara-Benerecetti AS (1985) Study of human red cell NADH diaphorase (DIA1) in the Italian populations. Hum. Hered. *35:*7–10.

Bernstein RF (1930) Fortgesetze Untersuchungen aus der Theorie der Blutgruppen. Z. Indukt. Abstammungs. Vererbungsl. *56:*233–273.

Biondi G, Calabrò V, Colonna Romano S, Giangregorio M, Malaspina P, Petrucci R, Santolamazza C, Santolamazza P, Tramontana E, and Battistuzzi G (1989) Common and rare genetic variants of human red blood cell enzymes in Italy. Anthropol. Anz. *47:*155–174.

Bissbort S, Ritter H, and Kompf J (1978) PGM1 subtyping by means of acid starch gel electrophoresis. Hum. Genet. *45:*175–177.

Brasili Gualandi P, Luiselli D, Gruppioni G, and Vona G (1993) Analysis of the polymorphism of haptoglobins in Sardinia. Int. J. Anthropol. *4:*195–204.

Casalis G (1836) Dizionario Geografico, Storico—statistico—Commerciale degli Stati di S.M. il Re di Sardegna. Bologna: Forni Editore.

Cavalli-Sforza LL, Menozzi P, and Piazza A (1994) The History and Geography of Human Genes. Princenton, NJ: Princenton University Press.

Chakraborty R, Kamboh MI, Nwankwo M, and Ferrel RE (1992) Caucasian genes in American Blacks: New data. Am. J. Hum. Genet. *50:*145–155.

Contu L, Arras M, Carcassi C, La Nasa G, and Mulargia M (1992) HLA structure of the Sardinian population: A haplotype study of 551 families. Tissue Antigens *40:*165–174.

Domenici R, Giari A, Bargagna M, and Weidinger S (1986) Distribution of C3 and Bf allotypes in Tuscany (Italy). Hum. Hered. *36:*330–332.

Ferraro G (1989) Da Tabarka a San Pietro. Cagliari: Tipografia Artigiana Musanti Editrice.

Floris G, and Vona G (1980) Isonimie maritale et coefficient de parenté entre six communes de l'Ile de Sardaigne. Anthopologie *84:*300–306.

Floris Masala R, Mameli GE, Succa V, and Vona G (1989) Distribuzione di marcatori genetici in alcune zone storico–geografiche della Sardegna. Rend. Semin. Fac. Sci. Univ. Cagliari *59:*203–216.

Gatti AM (1990) L'area di scambi matrimoniali in Sardegna tra XVII e XX secolo. In AA.VV.: Famiglia e Matrimonio nella Società Sarda Tradizionale. Nuoro: La Tarantola Edizioni, pp. 170–191.

Germenis A, and Babionitakis A (1982) Rapid phenotyping of C3 by immunofixation on cellulose acetate strips. Vox Sang. *43:*55–56.

Griffo RM (1988) Struttura genetica e linguistica della Sardegna. Tesi di laurea. Università di Torino (Italy).

Gruppioni G, Brasili Gualandi P, and Vona G (1991) Research on the distribution of properdin factor B in Sardinia. Gene Geogr. *5:*95–102.

Grunbaum BW (1981) Forensic Individualization of Human Blood. Gottingen: Sartorius Gmbh.

Harris H, and Hopkinson DA (1976) Handbook of Enzyme Electrophoresis in Human Genetics. Amsterdam: North-Holland Publishing Company.

I.S.T.A.T. (1993) Censimento generale dell'industria, commercio e popolazione.

Lucarelli P, Jannetti P, Palmarino R, Ruberto V, and Scarabino R (1973) Studio della 6-fosfogluconato-deidrogenasi nella popolazione di Roma. Rend. Accad. Naz. Lincei *54:*139–142.

Luxoro E (1977) Tabarka e Tabarkini. Cagliari: Edizioni Della Torre.

Marini E (1990) La scelta matrimoniale nel comune di Aritzo (Sardegna). Rend. Semin. Fac. Sci. Univ. Cagliari *60:*203–210.

Modiano G, Terrenato L, Santachiara-Benerecetti SA, Ulizzi L, Santolamazza C, Petrucci R, and Santolamazza P (1986) Population genetics in Sardinia. Atti Accad. Naz. Lincei Mem. *18*:257–330.

Montiel MD, Carracedo A, Lopez-Rodriguez MS, Rodriguez-Calco MS, Concheiro L, Huget E, and Gene M (1988) Comparison between isoelectric focusing methods for the detection of orosomucoid phenotypes. Electrophoresis *9*:268–272.

Moral P, Marogna G, Salis M, Succa V, and Vona G (1994) Genetic data on Alghero population (Sardinia): Contrast between biological and cultural evidence. Am. J. Phys. Anthropol. *93*:441–453.

Morelli L, and Vona G (1993) Studio genetico della popolazione di Villanova Monteleone (Sardegna). Nota I: Struttura matrimoniale. Rend. Semin. Fac. Sci. Univ. Cagliari *63*:75–86.

Moroni A, Anelli A, Anghinetti W, Lucchetti E, Rossi O, and Siri E (1972) La consanguineità umana nell'isola di Sardegna dal secolo XVIII al secolo XX. Ateneo Parmense *8*:47–63.

Piazza A, Mayr WR, Contu L, Amoroso A, Borelli I, Curtoni SE, Marcello C, Moroni A, Olivetti E, Richiardi P, and Ceppellini R (1985) Genetic and population structure of four Sardinian villages. Ann. Hum. Genet. *49*:47–63.

Piazza A, Olivetti E, Barbanti M, Reali G, Domenici R, Giari A, Benciolini P, Caenazzo L, Cortivo P, Bestetti A, Bonavita V, Crinò C, Pascali VL, Fiori A, and Bargagna M (1989) The distribution of some polymorphisms in Italy. Gene Geogr. *3*:69–138.

Reynolds J, Weir BS, and Cockerham CC (1983) Estimation of coancestry coefficient: Basis for a short-term genetic distance. Genetics *105*:767–779.

Roychoudhury AK, and Nei M (1988) Human Polymorphic Genes World Distribution. Oxford: Oxford University Press.

Saitou N, and Nei M (1987) The neighbor-joining methods: A new method for reconstructing phylogenetic trees. Mol. Biol. Evol. *4*:406–425.

Scacchi R, Palmarino R, Lucarelli P, Corbo RM, and Bajorek M (1987) PGM1 and Tf subtypes and C3 polymorphisms in Continental Italy and Sardinia. Data on the world distribution of these genetic markers. Int. J. Anthropol. *2*:47–60.

Seefried-Lehmann SJ, Walter H, Danker-Hopfe H, Rickards O, and De Stefano GF (1992) Investigation on the variability of four genetic serum protein markers (HP; TF; GC and PI subtypes) in Italy. Z. Morphol. Anthropol. *79*:215–231.

Sokal RR, and Rohlf FJ (1969) Biometry. San Francisco: Freeman.

Succa V, Mameli GE, and Vona G (1990) Gene markers and altimetry in Sardinia. Rend. Semin. Fac. Sci. Univ. Cagliari *2*:189–198.

Ulizzi L, Scozzari R, Stefanini R, Di Cori L, Salzano F, Santolamazza C, Santachiara Benerecetti SA, Beretta M, Bernini L, Van Loghem E, Nijehuis LE, Modiano G, and Terrenato L (1988) Genetic heterogeneity in Sardinia: 15 polymorphisms examined in 11 isolates. Gene Geogr. *2*:141–157.

Vallebona G (1974) Storia di una Colonizzazione. Cagliari: Edizioni Della Torre.

Vallebona G (1975) Evoluzione della Società Carlofortina. Cagliari: Editrice Sarda Fossataro.

Vona G, Floris Masala R, Mameli GE, and Succa V (1992) Red cell and serum protein polymorphisms in Sardinia. Int. J. Anthropol. *7*:25–33.

Walter H, Matsumoto H, and De Stefano GF (1991) Gm and Km allotypes in four Sardinian population samples. Am. J. Phys. Anthropol. *86*:45–50.

Workman PL, Lucarelli P, Agostino R, Scarabino R, Scacchi R, Carapella E, Palmarino R, and Bottini E (1975) Genetic differentiation among Sardinian villages. Am. J. Phys. Anthropol. *43*:165–176.